Joint effects of brood size and resource availability on sibling competition

Joint effects of brood size and resource availability on sibling competition

Daniel J. Sieber, Matthieu Paquet, Per T. Smiseth*

Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, U.K.

Received 25 November 2016

Initial acceptance 4 January 2017

Final acceptance 12 April 2017

MS number 16-01034R

*Correspondence: P. T. Smiseth, Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Charlotte Auerbach Road, Edinburgh, EH9 3FL, U.K.

E-mail address: per.t.smiseth@ed.ac.uk

The evolution of sibling competition is promoted when the brood's demand for resources (brood size) exceeds the parents' supply of resources (resource availability). However, little is known about the joint effects of brood size and resource availability and whether these effects are independent of each other. We conducted a study on the burying beetle *Nicrophorus vespilloides*, in which we manipulated both brood size and resource availability. We manipulated brood size by providing parents with 5, 10 or 20 larvae and resource availability by providing parents with a 5, 10 or 20 g mouse carcass. We found that resource availability had positive effects on parental food provisioning, larval body mass and larval survival, while brood size had a negative effect on larval body mass and larval survival. There were positive effects of the interaction between brood size and resource availability on larval begging and larval body mass, suggesting that the slopes describing the effect of brood size on larval begging and larval body mass became less negative as carcass size increased. When we repeated the analysis using larval density (i.e. brood size/resource availability) as a proxy for the shortage of resources, there were negative effects on parental care, larval body mass and larval survival. Our results have important implications by showing that there were main effects of both brood size and resource availability, and that their effects were not always independent of each other. Thus, treating brood size and resource availability as independent factors is preferential to using offspring density.

Keywords: begging, demand for resources, offspring density, parental food provisioning, sibling rivalry, supply of resources

Sibling competition is defined as any offspring trait that increases an individual offspring's fitness at the expense of the fitness of its siblings (Mock & Parker, 1997). Species with parental care often have intense sibling competition (e.g. annelids: Burd, Govedich & Bateson, 2006; insects: Kölliker 2007; Smiseth, Lennox & Moore, 2007; birds: Byholm, Ruosi & Sole, 2011; Bebbington, Kingma, Fairfield, Spurgin, Komdeur & Richardson, 2017; mammals: Hofer & East 2008; Andersen, Nævdal & Bøe, 2011), often occurring through sublethal scramble competition (begging) or lethal aggressive brood reduction (siblicide) (Mock & Parker, 1997; Roulin & Dreiss, 2012). The key ecological factor favouring sibling competition is limitation of resources critical for offspring development, such as food (Mock & Parker, 1997; Roulin & Dreiss, 2012). Resource limitation is often a consequence of parental overproduction of offspring, which may be adaptive if it allows the parent to (1) take advantage of favourable but unpredictable ecological conditions, (2) produce additional marginal offspring that enhance the fitness of core offspring (e.g. by assisting in thermoregulation or serving as food), or (3) produce replacement offspring should core offspring die (Mock & Forbes, 1997). Nevertheless, parental overproduction leads to a mismatch between the brood's total demand for resources and the parent's supply of resources, and sibling competition is promoted when the brood's total demand for resources (i.e. brood size) exceeds the parent's supply of resources to the brood (i.e. resource availability) (Mock & Parker, 1997).

Although there is general agreement that sibling competition is favoured when the brood's demand for resources exceeds the supply of parental resources (Mock & Parker, 1997; Roulin & Dreiss, 2012), relatively little is known about the joint effects of brood size and resource availability on the outcome of sibling competition. In the simplest scenario, both brood size and resource availability affect the outcome of

sibling competition and their effects are independent of each other. More complex scenarios occur when brood size and resource availability have different effects on the outcome of sibling competition and/or when the effect of brood size is conditional upon that of resource availability. For example, in great tits, *Parus major*, parents respond to an increase in brood size by increasing their provisioning rates such that this fully compensates for the increase in brood demand. Yet, despite the increase in resource availability matching the increase in brood size, offspring beg at substantially higher levels in enlarged broods than in control broods (Neuenschwander, Brinkhof, Kölliker & Richner, 2003). Thus, in this species, brood size promotes sibling competition despite the supply of resources to each offspring remaining constant. Considering this, it is now timely to investigate the joint effects of brood size and resource availability on sibling competition.

Here we investigated how brood size and resource availability influence sibling competition in the burying beetle *Nicrophorus vespilloides*. We used this species because it breeds on carcasses of small vertebrates, which serve as the only source of food for the developing larvae (Eggert & Müller, 1997; Scott, 1998). Thus, it is relatively straightforward to manipulate resource availability by simply varying the size of the carcass parents are given at the start of breeding (Smiseth & Moore, 2002; Smiseth, Andrews, Mattey & Mooney, 2014). Furthermore, there is no direct kin recognition of offspring by parents (Müller & Eggert, 1990), allowing us to manipulate brood demand by generating experimental broods of different sizes (Smiseth, Lennox & Moore, 2007; Pilakouta, Sieber & Smiseth, 2016). Although previous work on this species has manipulated either brood size or resource availability, no prior studies have manipulated both. Previous work on this species shows that siblings compete through sublethal scramble competition, either by

begging for food from parents or by self-feeding directly off the carcass (Smiseth, Lennox & Moore, 2007; Schrader, Jarrett, & Kilner, 2015).

The aim of this study was to investigate how variation in brood size and resource availability shapes the level of sibling competition in *N. vespilloides*. To address this issue, we manipulated both resource availability and brood size by providing parents with a 5, 10 or 20 g mouse carcass and a brood comprising 5, 10 or 20 larvae. We then monitored the subsequent effects on offspring and parental behaviour (i.e. larval begging and direct care by the female) and offspring performance (i.e. larval body mass and survival at dispersal from the carcass). We focused on sibling competition in the presence of a caring parent because this is the normal condition under which larvae compete for food (one or both parents normally provide care for the brood; Eggert & Müller, 1997; Scott, 1998). We tested for main effects of both brood size and resource availability and for effects of the interaction between them on offspring and parental behaviour and offspring performance. We then repeated the analyses using larval density (i.e. brood size/carcass size) as a proxy for the shortage of resources to the brood (Schrader, Jarrett & Kilner, 2015). We did this to examine whether the conclusions from these analyses were similar to those where we treated brood size and resource availability as two separate treatments.

<H1>METHODS

<*H2*>*Study Species*

Once parents have located a suitable carcass for breeding, they start burying it into the ground. They then remove any fur or feathers, deposit antimicrobial secretions onto the surface of the carcass, and females lay an average of around 30 eggs in the soil around it (Eggert, 1992; Scott, 1998; Smiseth, Ward & Moore, 2006). When the eggs

hatch approximately 60 h later (Smiseth, Ward & Moore, 2006), the larvae crawl to the carcass and start feeding within the crater created by the parents on top of the carcass. The larvae can self-feed, but also obtain food by begging for predigested carrion from the parents (Smiseth, Darwell & Moore, 2003). Although both parents typically provide care, females often stay on the carcass for longer and spend more time provisioning food to the larvae than males (Eggert, Reinking & Müller, 1998; Smiseth & Moore, 2002; Smiseth, Dawson, Varley & Moore, 2005). Larvae disperse from the carcass about 5 days after hatching, which corresponds to the end of the parental care period. Larvae pupate about 10 days after dispersal and eclose as adults about 10 days after pupation.

<H2>Study Population and Animal Husbandry

We used virgin beetles from an outbred laboratory population maintained at the University of Edinburgh, U.K. The beetles used in this study descended from beetles that were originally collected in Edinburgh, U.K. and Warmond, The Netherlands. The beetles were housed individually in transparent plastic containers (12 x 8 cm and 2 cm deep) filled with moist soil and kept at 20 ± 2 °C under a 16:8 h light:dark cycle. Nonbreeding adults were fed raw organic beef twice a week.

<H2>Experimental Design and General Procedures

To test for effects of brood size and resource availability on the outcome of sibling competition, we manipulated both the availability of parental resources (i.e. carcass size) and the brood's total demand for resources (i.e. brood size). Beetles selected for breeding were transferred to transparent plastic containers (17 x 12 cm and 6 cm deep) filled with 1 cm of moist soil and provided with a previously frozen mouse

carcass (Livefoods Direct Ltd, Sheffield, U.K.). We manipulated resource availability by providing parents with a 5 g (4.0–6.0 g), 10 g (9.0–11.0 g) or 20 g (19.0–21.0 g) mouse carcass at the start of the experiment.

Immediately after the eggs were laid, we removed the male and moved the female and the carcass to a new container with fresh, moist soil. We removed the males because the amount of care provided by the male is highly variable and male removal has no effect on offspring fitness under laboratory conditions (Eggert, Reinking & Müller, 1998; Smiseth, Dawson, Varley & Moore, 2005). We left the females to provide care for the brood because previous work on this species showed that sibling competition reduces offspring fitness only when larvae compete by begging for food from a parent (Smiseth, Lennox & Moore, 2007; Smiseth, Ward & Moore, 2007).

When the eggs started hatching, we manipulated brood size by providing parents with a brood comprising 5, 10 or 20 larvae. We used the newly hatched larvae to generate the experimental broods. All experimental broods included larvae of mixed maternity in accordance with established protocols (Smiseth, Lennox & Moore, 2007; Pilakouta, Sieber & Smiseth, 2015). This brood size manipulation is within the natural variation of brood size in *N. vespilloides* (mean ± SD: 21 ± 10 larvae, range 2–47 larvae; Smiseth & Moore, 2002).

Each experimental brood was randomly assigned to an unrelated female foster parent. In this species, parents cannot distinguish between unrelated foster broods and their own broods if the larvae are at the same developmental stage (Müller & Eggert, 1990). As parents kill any larvae that arrive on the carcass before their eggs are expected to hatch (Müller & Eggert, 1990), we only provided females with a brood once their own eggs had hatched. Females were left to care for their brood until the

larvae dispersed from the carcass about 5 days later.

<H2>*Offspring and Parental Behaviours*

We did the behavioural observations 24 h after the larvae were placed with a foster parent to coincide with the peak in larval begging and parental care (Smiseth, Darwell, & Moore, 2003). We recorded begging and female care following established protocols, using instantaneous sampling every 1 min over a period of 30 min (Smiseth & Moore, 2002, 2004a). At each scan, we recorded the number of larvae that were begging at that time point. We considered a larva to be begging when raising its head towards the parent and touching the parent with its legs (Rauter & Moore, 1999). Because larvae beg only when a parent is close, we noted the number of scans in which the female and larvae were in close proximity, defined as a distance of less than the female's pronotum width, corresponding to the approximate distance from the parent at which the larvae start begging (Rauter & Moore, 1999; Smiseth & Moore, 2002). At each scan, we also recorded the number of times the female was observed providing direct care, defined as when she was provisioning food to the larvae (engaging in mouth-to-mouth contact with at least one larva), interacting with the larvae (standing still within the crater and allowing the larvae to beg), or consuming carrion (feeding from within the crater; Walling, Stamper, Smiseth & Moore, 2008; Andrews, Kruuk & Smiseth, 2017).

<H2>*Offspring Performance*

At the time of dispersal from the carcass (about 4–6 days after hatching), we counted the surviving larvae in each brood. We also weighed the whole brood and calculated the average larval body mass for each brood by dividing brood mass by brood size.

190

<H2>Statistical Analysis

All analyses were performed using R version 3.0.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). For each of the four response variables of interest (larval begging, direct care by the female, larval body mass and
195 larval survival), we tested for main effects of brood size (i.e. 5, 10 or 20 larvae) and resource availability (i.e. 5 g, 10 g or 20 g carcass) as well as for the effect of their interaction. In all analyses, we treated brood size and resource availability as continuous variables. We also tested for an effect of larval density, defined as the number of larvae per g carcass (i.e. brood size/carcass size), which we also treated as
200 a continuous variable (ranging from 0.25 to 4 larvae per g carcass). To investigate the effects of carcass size, brood size and larval density on the proportion of time spent begging by a larva, we used generalized linear models with a quasibinomial distribution (glm, package stats). In models with direct care as the response variable, we used zero inflated linear models (glmmadmb, package glmmADMB for negative
205 binomial distributions) due to the high proportion of females that did not provide direct care during the observation period. To test for effects of brood size, resource availability and larval density on larval survival, we used generalized linear models with a quasibinomial distribution (glm, package stats). We used linear models (lm function in package stats) to test for effects of brood size, resource availability and
210 larval density on average larval weight and brood size at dispersal. We analysed all proportional data on larval begging and larval survival using the 'cbind' function in R given that it considers both the number of larvae that were begging and the number not begging in the brood, or the number of larvae that were alive and the number dead at dispersal (Crawley, 2005).

The total sample size in the experiment was $N = 185$ broods, which corresponds to the sample size for the analysis of larval survival. The sample sizes for the analysis on other traits were lower (Fig. 1). In the analyses on begging, we excluded 86 cases where the female spent no time close to the larvae. These cases provide no information on larval begging given that larvae only beg when the female is in close proximity (Smiseth & Moore 2002, 2004b). In addition, we excluded one brood from the analyses on begging because it had an abnormally high level of begging (15 of 20 larvae were begging at the only sampling point when the female was in close proximity). We excluded 19 cases in the analysis on direct care because the female had deserted the brood, and we excluded 11 cases in the analysis on larval body mass because all larvae died before the time of dispersal.

<H2>Ethical Note

Our study adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, the legal requirements of the U.K., as well as all institutional guidelines at The University of Edinburgh. None of the procedures used in this study had the potential to cause pain or distress to the beetles.

<H1>RESULTS

<H2>Brood size and resource availability

We found that there were no significant main effects of either brood size or carcass size on larval begging (brood size: estimate ± SE: -0.0012 ± 0.0137; $F_{96} = 1.62$, $P = 0.207$; carcass size: estimate ± SE: 0.0169 ± 0.0133; $F_{96} = 0.008$, $P = 0.929$; Fig. 1a). However, there was a significant positive effect of the interaction between brood size and carcass size (estimate ± SE: 0.00661 ± 0.00218; $F_{94} = 9.35$, $P = 0.003$),

suggesting that the slope describing the effect of brood size on larval begging became less negative as carcass size increased (Fig. 1a). Carcass size had a positive effect on the amount of direct care provided by the female: an increase in carcass size was associated with an increase in the amount of direct care (estimate ± SE: 0.0519 ± 0.0174; $\chi^2 = 8.56$, $P = 0.003$; Fig. 1b). There was no evidence, however, that brood size affected the amount of direct care by the female (estimate ± SE: -0.0130 ± 0.0192, $\chi^2 = 0.09$, $P = 0.759$), and there was no effect of the interaction between brood size and carcass size (estimate ± SE 0.00147 ± 0.00280; $\chi^2 = 0.27$, $P = 0.602$; Fig. 1b).

We found that brood size and carcass size had opposite main effects on larval body mass: an increase in brood size was associated with reduced larval body mass (estimate ± SE: -3.06 ± 0.36; $F_{171} = 115.15$, $P < 0.0001$) while an increase in carcass size was associated with increased larval body mass (estimate ± SE: 4.68 ± 0.37; $F_{171} = 70.80$, $P < 0.0001$; Fig. 1c). In addition, there was a positive effect of the interaction between brood size and carcass size (estimate ± SE: 0.181 ± 0.057; $F_{170} = 9.98$, $P = 0.002$), suggesting that the slope describing the effect of brood size on larval survival became less negative as carcass size increased (Fig. 1c). Brood size and carcass size also had opposite effects on larval survival: an increase in brood size led to lower survival (estimate ± SE: -0.0350 ± 0.0155; $F_{182} = 5.25$, $P = 0.023$) while an increase in carcass size led to higher survival (estimate ± SE: 0.124 ± 0.018; $F_{182} = 56.97$, $P < 0.0001$; Fig. 1d). However, there was no evidence of an effect of the interaction between brood size and carcass size (estimate ± SE: -0.00290 ± 0.00324; $F_{181} = 0.83$, $P = 0.364$; Fig. 1d).

<H2>Larval density

There was no significant effect of larval density (i.e. brood size/carcass size) on larval begging (estimate ± SE: -0.120 ± 0.089; $F_{96} = 1.91$, $P = 0.170$; Fig. 2a). However, an increase in larval density was associated with a significant decrease in the time spent providing direct care by the female (estimate ± SE: -0.298 ± 0.104; $\chi^2_{94} = 8.12$, $P = 0.004$; Fig. 2b). Finally, we found that larval density had a negative impact on both larval body mass (estimate ± SE: -32.7 ± 2.2; $F_{172} = 214.98$, $P < 0.0001$; Fig. 2c) and larval survival (estimate ± SE: -0.521 ± 0.081; $F_{183} = 41.94$, $P < 0.0001$; Fig. 2d).

<H1>DISCUSSION

Although there were no main effects of either brood size or resource availability on larval begging, we found evidence for a positive effect of the interaction between brood size and carcass size. We monitored such effects because begging represents a form of scramble competition among siblings (Parker, Royle & Hartley, 2002). For example, previous work on this and other systems shows that, although offspring use begging to signal their needs to the parents (Kilner & Johnstone, 1997; Smiseth & Moore, 2004b), offspring also adjust their begging behaviour to the number of competitors in the brood (e.g. Neuenschwander, Brinkhof, Kölliker & Richner, 2003; Smiseth, Lennox & Moore, 2007). Thus, our study provides insights into how offspring adjust their competitive behaviour in response to brood size and resource availability. Our results show the offspring's response to brood size was conditional upon resource availability; that is, the effects of brood size and resource availability were not independent of each other. It is not straightforward to interpret this interaction effect. However, previous work shows that larvae spend less time begging as brood size increases, presumably reflecting higher levels of interference when competing for food from the parents (Smiseth, Lennox & Moore, 2007). Thus, the

positive parameter estimate suggests that the slope describing this reduction in begging with brood size was more pronounced on smaller (5 g) carcasses than on larger ones (10 and 20 g). Further work is needed to examine why the offspring's response to brood size was conditional upon resource availability.

We found no evidence that female *N. vespilloides* adjusted the amount of direct care in response to brood size. Instead, we found that females provided more direct care as carcass size increased (Fig. 1b). We monitored effects on parental care because previous work on other systems shows that parents may compensate for brood size manipulations by adjusting their food provisioning (e.g. Neuenschwander, Brinkhof, Kölliker & Richner, 2003). Our results provide evidence for differential effects of resource availability and brood size on the amount of direct care by the female. This may reflect that resource availability in this species is limited by the size of the carcass acquired prior to breeding. Although females can facilitate larval growth and survival by providing more direct care (Andrews, Kruuk & Smiseth, 2017), they cannot increase the total supply of resources to the brood. In contrast, parents of birds and mammals can increase the total supply of resources to the brood in response to an increase in brood size either by extracting more energy from their stored energy reserves (mammals) or by providing additional food from the surrounding environment (birds). Thus, interspecific responses by parents to brood size and resource availability may vary depending on whether the resource used for breeding is finite as in *N. vespilloides* or not as in birds and mammals.

We found evidence for main effects of both brood size and resource availability on two key aspects of offspring performance: larval body mass and larval survival. Carcass size had a positive impact on larval body mass and larval survival, while brood size had a negative impact on larval body mass and larval survival. Our

results show that the main effects of brood size and resource availability were in the opposite direction of each other, as expected if sibling competition is promoted when the brood's total demand for resources (i.e. brood size) exceeds the parent's supply of resources to the brood (i.e. resource availability; Mock & Parker, 1997). Our results are consistent with previous work on other species with parental care reporting main effects of either brood size or resource availability. For example, increasing brood size has a negative effect on nestling growth and/or survival in common kestrels, *Falco tinnunculus* (Dijkstra, Bult, Bijlsma, Daan, Meijer & Zijlstra, 1990), marsh tits, *Poecile palustris* (Nilsson & Gårdsmark, 2001), great tits (Neuenschwander, Brinkhof, Kölliker & Richner, 2003), bank voles, *Myodes glareolus* (Koskela 1998), domestic pigs, *Sus scrofa* (Andersen, Nævdal & Bøe, 2011), European earwigs, *Forficula auricularia* (Kölliker, 2007) and our study species *N. vespilloides* (Smiseth, Lennox & Moore, 2007). In contrast, supplementation of additional resources has a positive effect on offspring growth and/or survival in greater snow geese, *Chen caerulescens* (White, Leclaire, Kriloff, Mulard, Hatch & Danchin, 2010), black-legged kittiwakes, *Rissa tridactyla* (Lindholm, Gauthier & Desrochers, 1994) and *N. vespilloides* (Smiseth, Andrews, Mattey & Mooney, 2014), while limitation of resources to the brood has a negative impact of offspring growth in bluethroats, *Luscinia svecica* (Smiseth, Bu, Eikenæs & Amundsen, 2003) and blue-footed boobies, *Sula nebouxii* (Drummond & Garcia Chavelas, 1989).

We found an effect of the interaction between brood size and resource availability on larval body mass. The positive parameter estimate suggests that the slope describing the effect of brood size on larval survival became less negative as carcass size increased (Fig. 1d). Such interaction effects might be expected given that a specific increase in brood size should have less of a negative impact when resources

are plentiful than when they are scarce. We found no evidence for such an interaction effect for larval survival. Thus, brood size and resource availability had independent effects on larval survival, but not on larval body mass. There is evidence for similar interaction effects as those reported here from studies on amphibians without parental care that manipulated both the number of larvae and the availability of resources (Hota & Dash, 1981; Ding, Lin, Fan & Ji, 2015). However, to our knowledge, this is the first study to provide evidence for such interaction effects in a species in which parents care for their offspring. Given that similar interaction effects may be widespread in species with parental care, there is now a need for further work on birds and other taxa with parental care that examines the joint effects of brood size and resource availability.

We repeated our analyses using larval density (i.e. brood size/carcass size) as a proxy for the shortage of resources to the brood. When doing so, we found negative effects of density on the amount of direct care by the female, larval body mass and larval survival. We found no effect of larval density on larval begging. This contrasts with our prior analyses treating brood size and resource availability as independent factors, which revealed a differential effect of brood size and resource availability on direct care by the female, and an effect of the interaction between brood size and resource availability on larval begging. Our results have important implications for the potential utility of offspring density (brood size/resource availability) as a proxy for the mismatch between supply and demand (e.g. Schrader, Jarrett & Kilner, 2015). Using offspring density would be justified if there are main effects of both brood size and resource availability and there are no effects of the interaction between the two. Our results show that that this is not always the case in *N. vespilloides* and suggest

that treating brood size and resource availability as independent factors is preferential to combining them into offspring density.

In sum, our study provides evidence for complex effects of brood size and resource availability on offspring begging, parental care and offspring performance. There were main effects of brood size and resource availability on offspring performance, differential effects on parental care, and effects of the interaction between them on larval begging and larval body mass. Nevertheless, our study leaves some unanswered issues. First, we focused on sibling competition, thus ignoring the potential for sibling cooperation (Forbes, 2007; Falk, Wong, Kölliker & Meunier, 2014). A recent study on our study species suggests that sibling cooperation occurs in the absence of caring parents (Schrader, Jarrett, & Kilner, 2015). Thus, one potential avenue for further work is to examine the joint effects of brood size and resource availability on sibling cooperation. Second, our study focused on the effects of specific values for brood size (5, 10 and 20 larvae) and resource limitation (5, 10 and 20 g carcasses). Although these values cover a wide range of both brood size and carcass size, they do not cover the full range of brood sizes (2–47 larvae; Smiseth & Moore, 2002) and carcass sizes (3.6–37.0 g) for this species. We note that our range for carcass size is greater than that of other studies on the same species (8–12 g; Schrader, Jarrett, & Kilner, 2015). Nevertheless, a potential avenue for further work is to examine the joint effects of brood size and carcass size across the full range of brood size and resource availability.

Acknowledgments

We thank Laura Crichton, Hannah Drummond, Lucy Ford, Ed Ivimey-Cook, Natalia Pilakouta and Ross Wotherspoon for their help with maintaining the stock population

of beetles at the University of Edinburgh. We thank the Institute of Evolutionary Biology at the University of Edinburgh for providing funds for the study. M.P. was funded by FYSSEN.

References

Andersen, I. L., Nævdal, E., Bøe, K. E. 2011. Maternal investment, sibling competition, and offspring survival with increasing litter size and parity in pigs (*Sus scrofa*). *Behavioral Ecology and Sociobiology, 65,* 1159–1167.

Andrews, C. P., Kruuk, L. E. B. & Smiseth, P. T. 2017. Evolution of parental care: phenotypic and genetic correlations between parent and offspring traits. *Behavioral Ecology, 28,* 39–48.

Bebbington, K., Kingma, S. A., Fairfield, E. A., Spurgin, L. G., Komdeur, J. & Richardson, D. S. 2017. Consequences of sibling rivalry vary across life in a passerine bird. *Behavioral Ecology* (in press).

Burd, M. Govedich, F. R. & Bateson, L. 2006. Sibling competition in a brood-tending leech. *Proceedings of the Royal Society B: Biological Sciences, 273,* 2461–2466.

Byholm, P., Ruosi, H. & Sole, I. 2011. Parental care in nesting hawks: breeding experience and food availability influence the outcome. *Behavioral Ecology, 22,* 609–615.

Crawley, M. J. 2005. Statistics: An Introduction using R. Chichester, U.K.: J. Wiley.

Dijkstra, C,, Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. 1990. Brood size manipulation in the kestrel (*Falco tinnunculus*): effects on offspring and parental survival. *Journal of Animal Ecology, 59,* 269–285.

Ding, G. H., Lin, Z. H., Fan, X. L. & Ji, X. 2015. The combined effects of food supply and larval density on survival, growth and metamorphosis of Chinese tiger

frog (*Hoplobatrachus rugulosa*) tadpoles. *Aquaculture, 435,* 398–402.

Drummond, H. & Garcia Chavelas, C. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour, 37,* 806–819.

Eggert, A.-K. 1992. Alternative male mate-finding tactics in burying beetles. *Behavioral Ecology, 3,* 243–254.

Eggert, A.-K. & Müller, J. K. 1997. Biparental care and social evolution in burying beetles: lessons from the larder. In J. E. Choe, & B. J. Crespi (Eds.), *The evolution of social behavior in insects and arachnids* (pp. 216–236). Cambridge, U.K.: Cambridge University Press.

Eggert, A.-K., Reinking, M. & Müller, J. K. 1998. Parental care improves offspring survival and growth in burying beetles. *Animal Behaviour, 55,* 97–107.

Falk, J., Wong, J. W. Y., Kölliker, M. & Meunier, J. 2014. Sibling cooperation in earwig families provides insights into the early evolution of social life. *American Naturalist, 183,* 547–557.

Forbes, S. 2007. Sibling symbiosis in nestling birds. *Auk, 124,* 1–10.

Hofer, H. & East, M. L. 2008. Siblicide in Serengeti spotted hyenas: a long-term study of maternal input and cub survival. *Behavioral Ecology and Sociobiology, 62,* 341–351.

Hota, A. K. & Dash, M. C. 1981. Growth and metamorphosis of *Rana tigrina* larvae: effects of food level and larval density. *Oikos, 37,* 349–352.

Kilner, R. & Johnstone, R. A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology and Evolution, 12,* 11–15.

Kölliker, M. 2007. Benefits and costs of earwig (*Forficula auricularia*) family life. *Behavioral Ecology and Sociobiology, 61,* 1489–1497.

Koskela, E. 1998. Offspring growth, survival and reproductive success in the bank

vole: a litter size manipulation experiment. *Oecologia, 115,* 379–384.

Lindholm, A., Gauthier, G. & Desrochers, A. 1994. Effects of hatch date and food supply on gosling growth in Arctic-nesting greater snow geese. *Condor, 96,* 898–908.

Mock, D. W. & Forbes, L. S. 1995. The evolution of parental optimism. *Trends in Ecology and Evolution, 10,* 130–134.

Mock, D. W. & Parker, G. A. 1997. *The evolution of sibling rivalry*. Oxford, U.K.: Oxford University Press.

Müller, J. K. & Eggert, A.-K. 1990. Time-dependent shifts between infanticidal and parental behavior in female burying beetles: a mechanism of indirect mother-offspring recognition. *Behavioral Ecology and Sociobiology, 27,* 11–16.

Neuenschwander, S., Brinkhof, M. W. G., Kölliker, M. & Richner, H. 2003. Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behavioral Ecology, 14,* 457–462.

Nilsson, J.-Å. & Gårdsmark, A. 2001. Sibling competition affects individual growth strategies in marsh tit, *Parus palustris*, nestlings. *Animal Behaviour, 61,* 357–365.

Parker, G. A., Royle, N. J. & Hartley, I. R. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. Ecology Letters, 5, 206–215.

Pilakouta, N., Sieber, D. & Smiseth, P. T. 2016. No evidence that sibling competition exacerbates inbreeding depression in a burying beetle. *Journal of Evolutionary Biology, 29,* 704–710.

Price, K. Harvey, H. & Ydenberg, R. 1996. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behaviour*, 51, 421–435.

Rauter, C. M. & Moore, A. J. 1999. Do honest signalling models of offspring solicitation apply to insects? *Proceedings of the Royal Society B: Biological Sciences, 266,* 1691–1696.

Roulin, A. & Dreiss, A. N. 2012. Sibling competition and cooperation over parental care. In N. J. Royle, P. T. Smiseth & Kölliker, M. (Eds.), *The evolution of parental care* (pp. 133–149). Oxford, U.K.: Oxford University Press.

Schrader, M., Jarrett, B. J. M. & Kilner, R. M. 2015. Parental care masks a density-dependent shift from cooperation to competition in burying beetle broods. *Evolution, 69,* 1077–1084.

Scott, M. P. 1998. The ecology and behavior of burying beetles. *Annual Review of Entomology, 43,* 595–618.

Smiseth, P. T. & Moore, A. J. 2002. Does resource availability affect offspring begging and parental provisioning in a partially begging species? *Animal Behaviour, 63,* 577–585.

Smiseth, P. T. & Moore, A. J. 2004a. Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behavioral Ecology, 15,* 621–628.

Smiseth, P. T. & Moore, A. J. 2004b. Signalling of hunger when offspring forage by both begging and self-feeding. *Animal Behaviour, 67,* 1083–1088.

Smiseth, P. T., Andrews, C., Mattey, S. N. & Mooney, R. 2014. Phenotypic variation in resource acquisition influences trade-off between number and mass of offspring in a burying beetle. *Journal of Zoology, London, 293,* 80–83.

Smiseth, P. T., Bu, R. J., Eikenæs, A. K. & Amundsen, T. 2003. Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. *Behavioral Ecology, 14,* 793–801.

Smiseth, P. T., Darwell, C. T. & Moore, A. J. 2003. Partial begging: an empirical model for the early evolution of offspring signalling. *Proceedings of the Royal Society B: Biological Sciences, 270,* 1773–1777.

Smiseth, P. T., Dawson, C., Varley, E. & Moore, A.J. 2005. How do caring parents respond to mate loss? Differential response by males and females. *Animal Behaviour, 69,* 551–559.

Smiseth, P. T., Lennox, L. & Moore, A. J. 2007. Interaction between parental care and sibling competition: parents enhance offspring growth and exacerbate sibling competition. *Evolution, 61,* 2331–2339.

Smiseth, P. T., Ward, R. S. J. & Moore, A. J. 2007. Parents influence asymmetric sibling competition: experimental evidence with partially dependent young. *Ecology, 88,* 3174–3182.

Walling, C. A., Stamper, C. E., Smiseth, P. T. & Moore, A. J. 2008. The quantitative genetics of sex differences in parenting. *Proceedings of the National Academy of Sciences of the United States of America, 105,* 18430–18435.

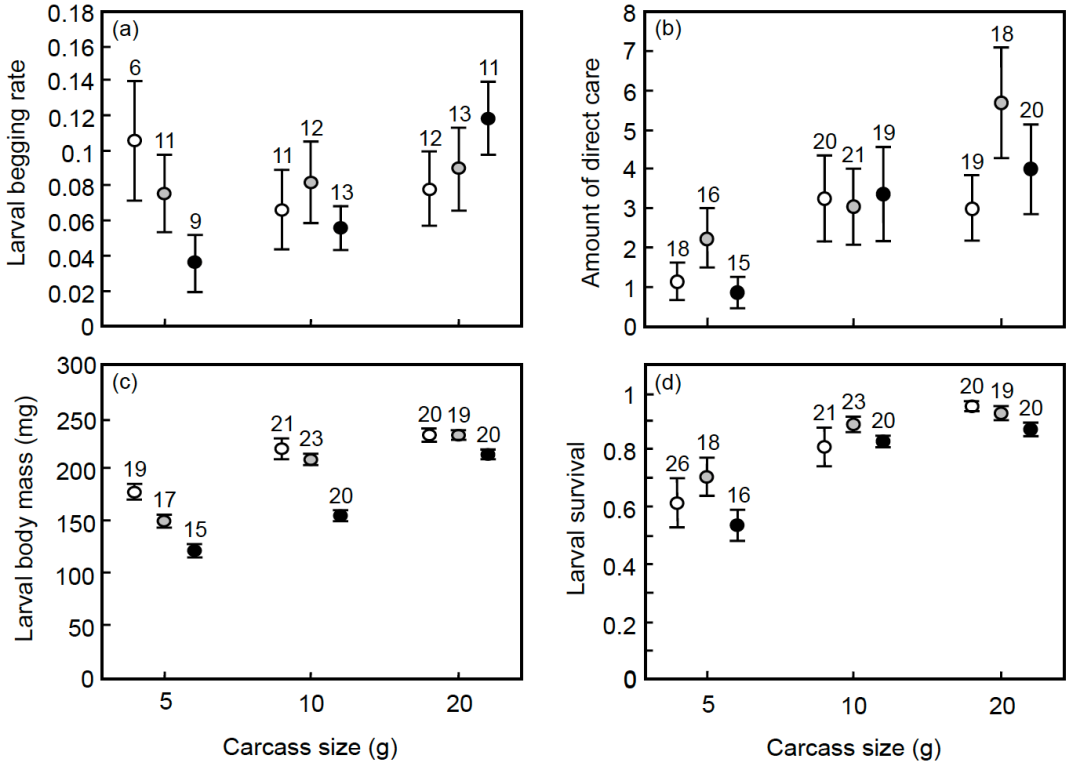
White, J., Leclaire, S., Kriloff, M., Mulard, H., Hatch, S. A. & Danchin, E. 2010. Sustained increase in food supplies reduces broodmate aggression in black-legged kittiwakes. *Animal Behaviour, 79,* 1095–1100.

Figure legends

Figure 1: Effects of brood size and resource supply (carcass size) on (a) the proportion of time spent begging by the larvae, (b) the time spent providing direct care by the female (number of scans out of 30), (c) larval body mass at dispersal (mg) and (d) the proportion of surviving larvae at dispersal. Variation in brood size is represented by points in different colours (white: 5 larvae; grey: 10 larvae; black: 20 larvae). Data reported as mean ± 1SE. Numbers above error bars represent sample size.

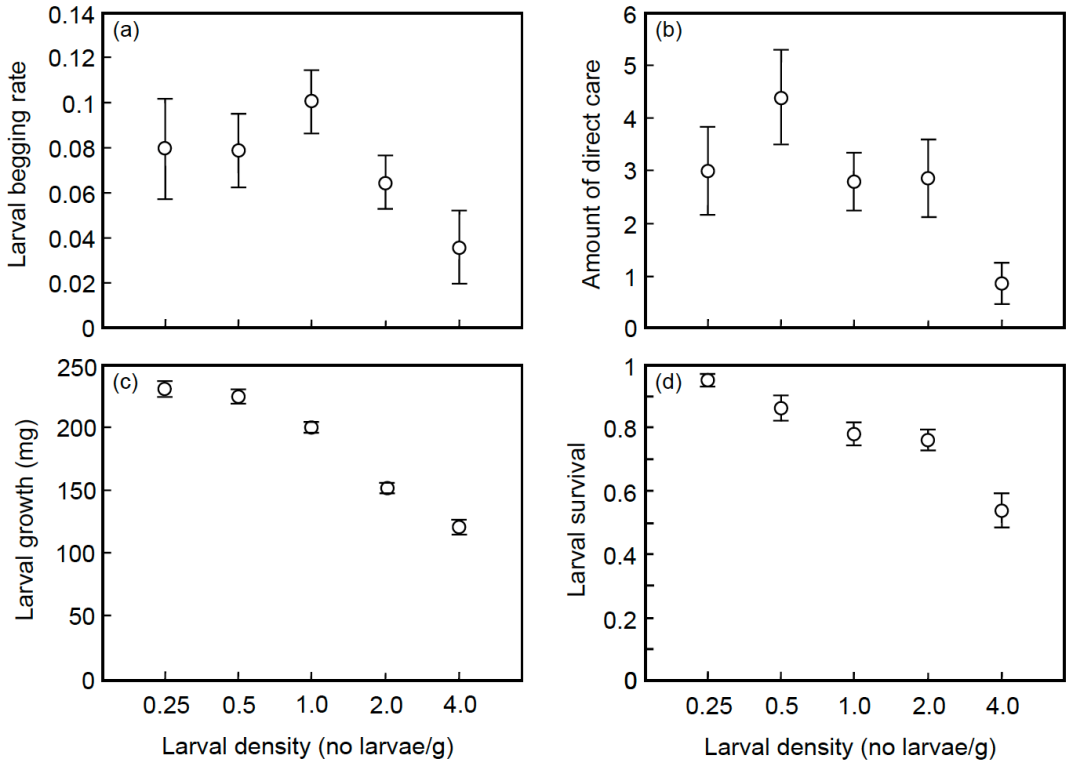
Figure 2: Effects of larval density on (a) the proportion of time spent begging by the larvae, (b) the time spent providing direct care by the female (number of scans out of 30), (c) larval body mass at dispersal (mg) and (d) the proportion of surviving larvae at dispersal. Larval density is calculated as number of larvae per g carcass. Data reported as mean ± 1SE.

[Figure 1]


(a)
Larval begging rate
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
6
11
9
11
12
13
12
13
11
(b)
Amount of direct care
8
7
6
5
4
3
2
1
0
18
16
15
20
21
19
19
18
20
(c)
Larval body mass (mg)
300
250
200
150
100
50
0
19
17
15
21
23
20
20
19
20
5
10
20
Carcass size (g)
(d)
Larval survival
1
0.8
0.6
0.4
0.2
0
26
18
16
21
23
20
20
19
20
5
10
20
Carcass size (g)

525

[Figure 2]


(a)
Larval begging rate
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
(b)
Amount of direct care
6
5
4
3
2
1
0
(c)
Larval growth (mg)
250
200
150
100
50
0
(d)
Larval survival
1
0.8
0.6
0.4
0.2
0
0.25
0.5
1.0
2.0
4.0
Larval density (no larvae/g)
Larval density (no larvae/g)